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Science Advice on Theoretical Harvest Reduction Scenarios and Sustainable Catches of NWA harp seals?

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

A population model was used to examine changes in the size of the Northwest Atlantic harp seal population between 1952 and 2014, and then extrapolated into the future to examine the impact of different harvest simulations on the modelled population. The estimates of 2014 population numbers at age, pup production, natural mortality (M), and carrying capacity (K) obtained from the fitting model were used as the starting point for the reduction scenarios. We were asked to determine the catches necessary to reduce the harp seal population to 6.8 million or 5.4 million animals assuming catches consisting of 90% Young of the Year (YOY) or 50% YOY, and occurred over different time periods (5, 10,and 15 years). Also, we were to determine the level of catches possible after each of these reduction scenarios that would be meet the management objective (i.e., a 95% probability of remaining above the Limit Reference Point which was defined as 2.4 million) for a period of 15 years. The impacts of different Canadian catch options on the projected population were tested under two scenarios. The first scenario (Model A) assumed that reproductive rates and Greenland catches were similar to that seen over the past 10 years. The second scenario, referred to as Model B, assumed that both future reproductive rates and Greenland catches behave in a density-dependent manner. The predicted changes in the population trajectory were affected very strongly by the age composition of the harvest used to reduce the population, the speed in which the reduction was achieved and whether the scenario used a population whose dynamics were assumed to be similar to what has been seen in the past 10 years or assumed to vary in a density-dependent manner.

The results of the modelling exercise indicated that more animals would need to be removed if the population reduction was to be achieved rapidly, or with a harvest comprised primarily of YOY. Under Model A, once the target level was achieved, the catch levels that would ensure a 95% probability of remaining above the Critical Reference Limit were much lower than the harvest levels allowable during the reduction phase. Under Model B, the numbers of animals needed to be removed to achieve the reduction target of 6.8 million animals, were similar to the numbers of animals needed to reduce the population to the same level, but under Model A. However, with Model B and a reduction target of 6.8 million animals), much higher harvests were allowed over the 15 years following the reduction due to the increased reproductive rates and reduced Greenland catch that were assumed. However, catch levels needed to reduce the population to 5.4 million were much higher when density dependence was assumed than under the Model A scenario and harvests had to be reduced considerably to permit the population to remain above the reference limit point. Under all scenarios, the uncertainty associated with estimates of population size increased considerably as time since the last survey also increased. These simulation results are very sensitive to model assumptions and should be considered for illustration only.

Avis scientifique sur les scénarios de réduction théorique des récoltes et des niveaux viables de prises de phoques du Groenland de l'Atlantique Nord-Ouest

RÉSUMÉ

Nous avons utilisé un modèle de population afin d'examiner les changements dans la taille de la population de phoques du Groenland de l'Atlantique Nord-Ouest entre 1952 et 2014, puis nous avons extrapolé les données afin d'examiner les effets simulés des différents niveaux de capture sur la population modélisée. Les estimations de la population selon l'âge en 2014, de la production de petits, de la mortalité naturelle (M) et de la capacité de charge (K) obtenues à partir de l'ajustement du modèle ont été utilisées comme point de départ pour les scénarios de réduction. Nous devions déterminer les captures nécessaires pour réduire la population de phoques du Groenland à 6,8 millions ou à 5,4 millions d'individus en supposant que les captures sont composées à 90 % de jeunes de l'année ou à 50 % de jeunes de l'année, et qu'elles ont eu lieu au cours de différentes périodes (5, 10 et 15 ans). De plus, nous devions déterminer le niveau de prises possible après chacun de ces scénarios de réduction qui permettrait d'atteindre l'objectif de gestion (p. ex., une probabilité de 95 % de rester au-dessus du point de référence limite, défini à 2,4 millions d'individus) pour une période de 15 ans. Les impacts des différentes options de captures canadiennes sur la population projetée ont été testés dans deux scénarios. Le premier scénario (modèle A) supposait que les taux de reproduction et les prises dans les eaux du Groenland étaient similaires à ceux observés au cours des dix dernières années. Le deuxième scénario (modèle B) supposait une hausse du taux de reproduction futur et des prises dans les eaux du Groenland d'une façon dépendante de la densité. Les changements prévus dans la trajectoire de la population ont été très affectés par la composition selon l'âge des phoques capturés dans le but de réduire la population, la vitesse à laquelle la cible de réduction a été atteinte, et si le scénario utilisait une population dont la dynamique était supposément comparable à celle observée au cours des dix dernières années ou supposément variable en fonction de la densité.

Les résultats de l'exercice de modélisation ont révélé qu'un grand nombre d'animaux devraient être prélevés si la réduction de la population doit être réalisée rapidement, ou si la récolte est composée principalement de jeunes de l'année. D'après le modèle A, une fois le niveau cible atteint, les niveaux de prises qui assureraient une probabilité de 95 % de rester au-dessus du point de référence limite critique étaient beaucoup plus faibles que les niveaux de prélèvement autorisés durant la phase de réduction. Selon le modèle B, le nombre d'individus devant être prélevé afin d'atteindre l'objectif de réduction de 6,8 millions d'individus était similaire au nombre d'individus nécessaires pour réduire la population au même niveau, mais selon le modèle A. Toutefois, selon le modèle B et un objectif de réduction de 6,8 millions d'individus, des prises beaucoup plus élevées ont été autorisées au cours des 15 années suivant la réduction en raison de l'augmentation du taux de reproduction et de la diminution des prélèvements groenlandais qui étaient hypothétiques. Cependant, les niveaux de capture nécessaires pour réduire la population à 5,4 millions d'individus étaient beaucoup plus élevés lorsque la dépendance à la densité était supposée que selon le scénario du modèle A, et les captures devaient être réduites considérablement pour permettre à la population de se maintenir au-dessus du point de référence limite. Dans tous les scénarios, l'incertitude entourant les estimations de la taille de la population augmentait considérablement au fil du temps, puisque les données tirées du dernier relevé ont aussi augmenté. Ces résultats de simulation sont très sensibles aux hypothèses du modèle et devraient être pris en compte aux fins d'illustration seulement.

INTRODUCTION

The harp seal *(Pagophilus groenlandicus)* is a medium sized, migratory phocid distributed over continental shelf regions of the north Atlantic. Three populations are recognized (Sergeant 1991); the White Sea/Barents Sea, the Greenland Sea and the Northwest Atlantic (NWA). All three populations have a long history of commercial and subsistence exploitation throughout their range. The NWA harp seal summers in the eastern Canadian Arctic and west Greenland, but migrates south in the fall to overwinter and reproduce on the pack-ice off northeastern Newfoundland (Front) and in the Gulf of St. Lawrence (Gulf) every spring (Sergeant 1991). The pups are weaned after a short lactation period of 12-14 days, but remain on the ice for another few weeks before dispersing (Sergeant 1991). This population has been harvested commercially since the 1700's (Sergeant 1991) and, until recently, this hunt was among the largest wildlife harvests in the world. The United States Whitetail deer (*Odocoileus virginianus*) and European roe deer (*Capreolus capreolus*) sport harvests are probably the largest, each removing over 2.5 million deer annually, followed by the Australian kangaroo (Macropus *sp*) hunt (1.5 million animals in 2010; Anon. 2012; Burbaite and Csányi 2009; QDMA 2014), but the Canadian commercial seal hunt is the largest harvest of marine mammals removing on average 211 000 seals annually between 1996 and 2013, increasing to an average of 407 000 seals annually if the Canadian and Greenland subsistence hunts, struck and loss, and incidental catches are also considered (Hammill et al. 2015). The harp seal is considered to be the most abundant pinniped in the North Atlantic and their status is one of continuing interest (e.g. Leaper et al. 2010; Marland 2014; Soulen et al. 2013). In addition to harvesting, harp seals play an important role in structuring the North Atlantic ecosystem (e.g. Morissette et al. 2006; Peacock et al 2013). Therefore, it is important that we have a good understanding of their abundance and population dynamics.

In Canada, harp seals are managed as a harvestable resource and in 2003, DFO adopted a management plan that incorporated the Precautionary Approach. The approach identifies Limit (or Critical) and Precautionary reference levels that can be used classify the 'health' of the population (Hammill and Stenson 2007). These reference levels are defined as a proportion of the maximum population (Nmax) with the Limit Reference Level (LRL) being 30% of Nmax and the Precautionary Reference Level (PRL) being 70% of Nmax. The current management objective is to maintain a population that has an 80% likelihood of remaining above the PRL, which is a proxy for the level that ensured a 95% likelihood of being above the LRL. In addition to their value as a resource, however, harp seals are also perceived to have potentially negative impacts on commercial fisheries as predators or competitors (e.g. Bousquet et al. 2014; Chassot et al. 2009). These two concerns can result in different objectives for the management of this population.

Therefore, Ecosystems and Fisheries Management has asked Science to examine the following questions that could be used for the purpose of discussion with stakeholders:

1. Identify the catches necessary to reduce the population to 5.4M animals assuming:
    a. Catches consisting of 90% Young of the Year (YOY) or 50% YOY
    b. Reductions over time periods of 5, 10, and 15 years
2. Identify the catches necessary to reduce the population to 6.8M assuming:
    a. Catches consisting of 90% YOY or 50% YOY
    b. Reduction over time periods of 5, 10, and 15 years

3. What would be the sustainable future catches possible at each of these reduced populations, assuming there is a 95% probability of remaining above the Limit Reference Point (defined as 2.4 million).

MATERIALS AND METHODS

We approached this request in 2 parts. In the first we estimated the current population and age structure and then, in the second, projected this population forward under different assumptions and catch levels.

The dynamics of the Northwest Atlantic harp seal population from 1952 -2014 were described by fitting a model to independent estimates of the total pup production, and reproductive rates observed for seals 8 years old and older (referred to as 8+)(Hammill et al. 2015). It was considered that the dynamics of the population can be described by assuming density dependent mortality acting on both juvenile survival and pregnancy rates of the 8+ individuals. It is also assumed that the sex ratio is 1:1. The model integrates data on removals and ice-related mortality, and was fit by adjusting initial population size (a), adult (i.e. one year old and older, referred to as 1+) mortality rates (M_{1+}) and the carrying capacity (K). We begin by presenting inputs to the population model, followed by an explanation of the model structure and fitting. Many of the data inputs are included in the Appendices and are presented in Hammill and Stenson (2011) and Hammill et al. (2011a, 2012, 2015).

FITTING MODEL

Data input

2.1.1 Pup production estimates

The model is fit to 12 independent estimates of pup production (Table 1) obtained from mark-recapture studies (Roff and Bowen 1986), and aerial surveys (Sergeant and Fisher 1960; Stenson et al. 1993, 2002, 2003, 2014a). The 1952 and 1960 surveys did not cover the entire area and approximated the number of pups in non-surveyed areas, but nonetheless are thought to provide useful information. We included these surveys, but assigned a high coefficient of variation (50%) to reflect the uncertainty in the estimates. The 1990-2012 surveys have used the same basic sampling design as described by Stenson et al. (1993, 2002, 2003).

2.1.2 Reproductive rates

Estimates of late term pregnancy rates ($P_{x,t}$) for animals at age x and in year t are available from sampling programs maintained by the Department of Fisheries and Oceans since 1954 (Sjare and Stenson 2010; Stenson et al. 2016). Samples represent late-term pregnancy rates since they are collected only a few months (October to February) prior to pupping in March. It is assumed that there would have been no mortality after the samples were taken and animals are entered into the model at the age they would have had at the time of pupping. Seals 3 years old and younger are considered immature while seals 8 years and older are considered to be fully recruited into the population. Only the reproductive rates of animals aged 8+ years was used in the model fitting because the larger sample size available for this group provided more reliable estimates.

The reproductive data were smoothed by applying a local logistic regression (Loader 1999) to the binary data (pregnant or non-pregnant; Tibshirani and Hastie 1987). This smoother yields errors around the predictions and allows weighting by sample size to take into account the local density of data. Thus, there is no need to exclude data points for which sample size is below an arbitrary threshold. A range of smoothing scales was explored and we selected the degree of

smoothing with the best fit, i.e., lowest AIC (Loader 1999). To compute confidence intervals, variance in the smoothed data was estimated using log-likelihood in the framework of normal approximations (Loader 1999). Using the binomial family kept pregnancy rates in the [0, 1] interval and resulted in non-symmetric errors around the mean. Smoothing was performed using the *R* package *LocFit* (Loader 2010).

The smoothed reproductive rates were extrapolated backwards from 1954 to 1952. Stenson *et al.* (2014b) explored the impact of sample size on estimates of fecundity. They found that the precision of the estimates stabilized at sample sizes of around 40 animals. Therefore, if the number of samples in a particular year and age class exceeded the threshold, then the observed reproductive rate and the associated uncertainty were used in the model. However, if the sample size for the reproductive tracts in a given year was below the threshold, then the model replaced the actual observed value with a value derived from the smoothing model for that year and age class. When the smoothed rates were used, uncertainty was incorporated by resampling pregnancy rates from a normal distribution in logit space, with a mean equal to the smoothed value and the standard error equal to the square root of the estimated variance.

2.1.3 Catches

Catch data ($c_{a,t}$) for age *a*, in year *t* are available since 1952 (Fig. 1; Stenson 2014). Data include the Canadian commercial harvest, the Canadian Arctic subsistence hunt, animals caught incidentally in Canadian and American commercial fisheries, and the Greenland subsistence hunt. Reported catch levels from the Canadian and Greenland hunts were divided into Young of the Year (YOY), which are seals less than 1 year of age and numbers of animals aged one year and older (1+). Catches of 1+ seals are distributed proportionally among the model estimates of the 1+ age classes. The proportion of YOY was approximately to be 3.4% of the animals in the Canadian subsistence hunt, while in the Greenland subsistence hunt the proportion of YOY averaged 59% from 1952-1977, declining to less than 20% since then (Stenson 2014). There is normally a two year delay in the collection of the Greenland harvest data. For the present exercise, data on Greenland catches were available up to and including 2011. For 2012 and 2013, the average catch for the last 10 years was used.

Corrections for seals killed but not reported (i.e. struck and lost), are incorporated into the model assuming that 95% of the YOY and 50% of the 1+ animals in the Canadian commercial hunt (Front and Gulf) are reported while 50% of all animals killed in Greenland and the Canadian Arctic are assumed not to have been recovered and/or reported (Spare and Stenson 2002). It was also assumed that 99% of the YOY in the Canadian commercial catch were reported prior to 1983.

2.1.4 Ice-related mortality of YOY

In some years, unusually high mortality of YOY can occur due to extremely poor ice conditions while the pups are still with the female or during the post weaning fasting period. Ice breakup results in the YOY dying due to being forced into the water. This mortality factor, actually included in the model as a survival term between 0 and 1, is incorporated in the model, prior to the beginning of hunting (Equation 2).

MODEL STRUCTURE

The initial population (Pop_{1952}) is entered as a vector of numbers of animals at age *x* (N_x)

$$Pop_{1952} = \sum_{x=1}^{26} (\alpha \times n_x) \qquad \text{(Equation 1)}$$

Where α is a multiplier that is adjusted during the model fitting process.

The number of animals ($n_{x,t}$) at age x in time t is related to survival in prior six years ($S_{x-6:t-1}$), catches ($c_{x,t-1}$), and a base pup mortality rate (M_0) which is defined as 3 times adult mortality ($\omega=3$) i.e. $M_0 = 3 \times M_{x>1}$ to allow for higher mortality of first year seals (for consistency with previous studies; Roff and Bowen 1983). Pup mortality was also assumed to be subject to density-dependent factors related to total population size N and the estimated carrying capacity (K) and theta (θ set at 2.4; Trzcinski et al. 2006):

$$n_{1,t} = ((n_{0,t-1} \times S_{0:t-1}) - c_{0,t-1}) \times e^{-M_0} \times (1 - (N_t/K)^\theta) \quad \text{(Equation 3)}$$

The number of animals age x, with $1 < x < X$ was related to mortality and catches:

$$n_{x,t} = \left(n_{x-1,t-1} \times e^{\frac{-M_{x>1}}{1}} - c_{x-1,t-1}\right) \times e^{\frac{-M_{x>1}}{1}} \quad \text{(Equation 5)}$$

while numbers for the terminal age class (n_X) is

$$n_{X,t} = \left[\left(n_{x-1,t-1} + n_{X,t-1}\right) \times e^{\frac{-M_{x>1}}{1}} - \left(c_{x-1,t-1} + c_{X,t-1}\right)\right] \times e^{\frac{-M_{x>1}}{1}} \quad \text{(Equation 6)}$$

The number of pups born in year t is described by the number of females ($n_{x,t}$, $x \geq 1$) considering a sex ratio of 1:1) at age (x) and age specific reproductive rates ($P_{x,t}$) in year t:

$$n_{0,t} = \sum_{x=1}^{X} n_{x,t} \times P_{x,t} \times 0.5 \quad \text{(Equation 5)}$$

It was felt that in years where good environmental conditions were encountered that these conditions would likely be experienced across all age classes and vice versa in poor years. We incorporated this feature of synchrony into the model using the function CorBin, a multivariate distribution composed of binomial distributions where the degree of correlation is controlled via an 8-dimension Gaussian copula (Oster 1999, Joe 1997, Trivedi and Zimmer 2005). In this function, $n_{x,t\,reproduct,t}$ corresponded to the sample size used to obtain the observed pregnancy rate for females at age x in year t, and $p_{x,t\,preg,t}$ was the proportion pregnant in the observed group in year t.

For age x, with $1 < x < 8$:

$$P_{x,t} \sim CorBin\left(n_{x,t\,reproduct,t}, P_{x,t\,preg,t}\right) \quad \text{(Equation 6)}$$

For age x, with $x \geq 9$ (i.e. 9+):

$$P_{x,t} = P_{9,t} \sim CorBin\left(n_{9+,t\,reproduct,t}, P_{9+,t\,preg,t}\right) \quad \text{(Equation 7)}$$

During the model fitting, the model samples from the distribution of pregnancy rates for the 9+ age class. If the reproductive rate is high, then the correlation ensures that higher values (depending on the strength of the correlation) for the other age classes will also be chosen. This synchrony increased uncertainty, since the model tends to show a mix of good and bad years for pregnancy. If reproduction was not correlated among age classes, then this reduced the variability in pup production since the high proportion of females pregnant in some age classes would be offset to some extent by lower pregnancy rates among other age classes. The model also assumes that pregnancy rates undergo density-dependent changes as the population nears carrying capacity. The predicted reproductive rates ($P_{9+,t}$) for animals aged 9+ years in year t is:

$$P_{9+,t} = 0.88 \times (1 - N_t/K)^\theta \quad \text{(Equation 8)}$$

Where $\hat{f}_{MSY}$ is the maximum reproductive rate observed for animals aged a, and $\hat{f}_a$ and $\hat{f}_0$ are defined as above equation (3).

MONTE CARLO RESAMPLING AND PARAMETER ESTIMATION

The model creates a population matrix with 28 age classes from 1900 until the current year. The initial age distribution vector (28×1) has values of 850 000, 599 000, 419 000, 275 000, 189 853, 312 171, 481 441, 452 555, 425 451, 388 871, 275 888, 303 332, 332 132, 314 256, 295 472, 270 953, 258 511, 245 703, 229 128, 215 380, 202 467, 190 316, 179 091, 169 126, 159 856, and 149 594. It was created as an initial population age structure with first year mortality assumed to be three times (Huff and Bowen 1999) the adult mortality rate of 0.06. Changes in this distribution have little impact on current estimates of pup production and the population (Hammill et al. 2015). The size of the initial population is adjusted by a multiplying factor (α; Equation 1). We included the uncertainty in the pregnancy rates and the pup production estimates in the fitting model by resampling the parameters using Monte Carlo techniques. At each iteration of the model, pregnancy rates are resampled for each year assuming a binomial distribution (correlated among age classes). Parameters of the binomial distributions were estimated directly from reproductive rate data when the number of reproductive samples exceeds a threshold of 40 (see section 2.1.3) or based on the smoothed estimate of pregnancy rates if the number of samples < 40. Pup production estimates from the surveys are resampled assuming a normal distribution (with variance based on estimates of the survey errors). For each iteration, the model minimizes the sum of squares (SSQ) of two objective functions:

$$SSQ = \left[\frac{\left(\ln(\text{Observed PUP counts}) - \ln(\text{Predicted PUP counts})\right)^2}{2\left(\ln(\text{SE of PUP counts})\right)^2}\right] + \left[\frac{\left(\ln(\text{Observed Catch}) - \ln(\text{Predicted Catch})\right)^2}{2\left(\ln(\text{SE of Catch})\right)^2}\right] \qquad \text{Equation 5}$$

by estimating three parameters: the initial population factor (α), the instantaneous mortality rate (M), and the carrying capacity (K). The three parameters (α, M and K) are optimized by iterative methods (for 10 000 iterations). For each Monte Carlo iteration, rates ($\hat{f}_a$, $\hat{f}_0$ and s) are estimated and stored. The model runs in the programming language R (R Core Team 2016). Results are specified as mean (±SE) unless stated otherwise. 95% confidence limits are presented as 2.5(2)75 and 2.5(2)97.5 quantiles, except for the 1951 and 1952 survey estimates which are estimated as ±1.96*SE.

PROJECTION MODEL

The second component of the model, referred to as the 'Projection Model', projects the population into the future to examine the impacts of different management options on the population. The projection model is based on the same equations as the fitting model, but uses as a starting point, the estimates of 2016 population size, pup production, rebuild mortality (M), and carrying capacity (K) obtained from the fitting model.

Assumptions associated with future reproductive rates and levels of the Greenland catch are also necessary. Therefore, we tested the impacts of the different Canadian catch options on the projected population under two major scenarios that represent a continuation of the current state and one that assume density dependent compensation. In the first scenario, which we refer to as Model A we assume future reproductive rates, and Greenland catches based upon the observed rates from the past 10 years (see below).

In the second scenario, which we refer to as Model B, both future reproductive rates and Greenland catches behave in a density dependent manner, i.e. as the population declines, Greenland catches decline and pregnancy rates increase to an asymptotic value, whereas when

the acquisition behaviours, vaccine hesitancy and reproductive value decline. Using this density-dependent approach, we then examined the impacts of the different harvest options on the projected population.

Management simulations

Including that the simulation examines specific scenarios:

1. Identify the catches necessary to reduce the population to 0.4B carrying capacity
   a. Catches ca. ~using of 95% (Young of the Year (YOY) ca 50% YOY
   b. Reduction occur over time periods of 5, 10, and 15 years
2. Identify the catches necessary to reduce the population to 0.6B carrying
   a. Catches containing of 95% YOY ca 50% YOY
   b. Reductions occur over time periods of 5, 10, and 15 years
3. What would be the sustainable harvest catches possible at each of these reduced populations, assuming there is a 90% probability of remaining above the Limit Reference Point (defined as 0.4 billion). This does not require that the population remain stable at the reduction target level.

In all scenarios we assume that the age structure and mortality from harvest and that it remains at the harvest levels between 2001 and 2011 (Appendix A). We also assume that the proportion of males (bull) and (cow), for the different harvest levels remain as estimate above for the fitting model.

Assumptions for the Model A scenarios

1. Investment catches were kept at 75,000 per year, which represents the midpoint in harvest levels between 2001 and 2011 (Appendix A).
2. Use related mortality annually, expressed as survival (s model), was assumed to vary randomly, with each run selecting one value with replacements, from 10 values that values drawn out over the past 10 years: (s = 0.96, 0.96, 1, 0.96, 0.97, 0.96, 0.96, 0.96, 0.97).
3. Reproductive rates did not change with population size (Model 1, but were allowed to vary randomly, with each run selecting a value for that age class with replacements from a vector of reproductive values, consisting of values observed over the last decade. For example, the values for animals 6 years and older (the percent, which for 90% of the age combination is: 0.96, 0.96, 0.97, 0.96, 0.96, 0.76, 0.76, 0.96, 0.96, 0.97).
4. Mortality rates of Young of the Year (YOY) were set to follow density-dependent dynamics, with YOY mortality increasing as the population approached carrying capacity, as (Equation 4).

Assumptions for Model B scenarios

1. Investment catches were assumed to be dependent on the harvestable population size. We determined a linear catch response rate curve in the investment catch rates using piecewise regression. In the first part, taking the breakpoint, investment catches were described by a linear relation with the total population size ( ). As the population size and is 40% predictive mean can be estimated around the estimated mean, assuming normal distribution of the error. In the second part of the relation ( ) when the total population size is larger than ( ) million individuals the catches were assumed to follow a uniform distribution centered on the mean investment catch estimate ( ) at the break point ( ). As 000 animals, with an range equal to the observed values (44,000 – 84,000).

ce. We attempted to capture the interannual variability by multiplying the reproductive rates by a variable we refer to as a food factor, which was chosen randomly from a vector of values obtained by estimating the ratio between the observed pregnancy rate and one predicted by the density dependent model over the past 10 years. This resulted in some years being higher than expected if reproduction was governed by density dependent factors alone, while in other years reproductive rates would have been lower than expected which is consistent with the observed changes in reproductive rates.

The model estimated how many animals would need to be removed to result in a lower harp seal population and then, once achieved, what level of harvests may be sustainable. As indicated above, these numbers are only valid within the context of the modelling scenarios examined in this study. Although we only examined a limited number of conditions, they represent two very different and contrasting scenarios; one assumed that reproductive rates, and ice conditions that have been observed over the last decade would persist into the future (Model A), while the second condition (Model B), assumed that density-dependent factors played a more important role in the dynamics of the population. The modelling showed that under all scenarios, the age composition of the harvest had a major impact on the numbers of animals that needed to be removed to achieve the management objectives and on the longer term dynamics of the population. For any significant reduction in the population to occur with catches similar to that seen in recent years, it must involve a significant proportion of animals that are age 1+ years. Removals consisting almost entirely of YOY animals would be unlikely to meet the management objectives or require catch levels not seen since the early 1960s (Hammill et al. 2015b). In both scenarios, Model A and Model B, similar numbers of animals would need to be removed to reduce the population to the target sizes. However, only relatively low harvests would still allow the population to remain above the Limit Reference Level in the case of the Model A model, while much higher harvests could be permitted in the case of a population whose dynamics were governed by density-dependent factors.

If the population was reduced to 5.4 million animals, we estimated that under most scenarios there would be a sharp reduction between the reduction harvest levels, and maintenance harvest levels that would still permit the population to remain above the Limit Reference Levels. No such major decline was observed for the population reduction to 6.8 million animals when density-dependence was assumed. The population model estimated a carrying capacity of approximately 10 million animals. In this study we used a shaping (theta) value of 2.4 (Trzcinski et al. 2006), which defines the Maximum Sustainable Yield or maximum productivity at approximately 64% of K, which would be 6.4 million animals. Thus reducing the population to 6.8 million animals, or near MSY values, would enable high productivity and high harvests, while still respecting the management objective. In contrast, reducing the population to 5.4 million would reduce the population to below MSY levels, resulting in a sharp decline in possible harvests in order to respect the management framework.

It should also be noted that the catch levels estimated to meet the management objective (95% likelihood of being above the Limit Reference Level) were only maintained for a period of 15 years while the impact of the removals on the population would continue well beyond this period. This is particularly obvious in Fig. 2 where continuing catches at even the reduce 'post-reduction' level would cause the population to continue to decline. To maintain the population above the LRL would require a more significant decrease in the allowable catches. If the management objective had been to maintain the population at the reduction target level, the 'post reduction' catches would have been much smaller.

The simulations were based on specific assumptions and that these conditions would persist over a period of 15 years beyond the population reduction period. It is extremely difficult to predict future directions of the population beyond one or two years because of uncertainties in

demographic parameters, harvest levels in both Canada and in Greenland, as well as changes in ice conditions for breeding and availability of food resources. One assumption that is extremely important is that adult mortality rates will remain constant over the duration of the simulation period. Any changes in this parameter will have major consequences on the dynamics of the population. Also, the two scenarios examined represent two unlikely situations, one assuming that catches and reproductive rates remain only within the range used in the projections, while the other assumes that reproductive rates and catches will compensate in some way (density-dependent response) as the population declines. Based upon historical changes in reproductive rates, we expect that some density dependent compensation will occur, but recent environmental changes suggest that full compensation may not result. The estimated carrying capacity is based upon historical conditions and may no longer be the same. Therefore, the results presented here are only valid within the context of the modelling scenarios examined in this study.

The simulations should also be viewed as potential outcomes in an ideal world where model assumptions and predictions behave in a manner described by the model, or as outlined in the basic scenario assumptions. They provide useful information to improve our understanding on how a population might respond if subject to a significant period of removals and to provide information on the implications of these population changes to future management objectives. However, only a limited range of scenarios was examined and real life changes in the population are likely to differ substantially from the simulation outcomes presented here.

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Table 1. Annual removals needed to reduce the population from current levels to 6.8 or 5.4 million within a period of 5, 10 or 15 years, assuming reproductive rates, Greenland harvests and ice-conditions persist within a range of conditions experienced over the last decade (Model A). Catches were assumed to comprise 90%, or 50% young of the year (YOY). Continuing removals represent the total annual removals allowed that would maintain a 95% likelihood that the population would remain above the limit reference level (N_{30}) for 15 years.

Scenario	90%YOY		50%YOY	
	Reduction ('000)	Continuing ('000)	Reduction ('000)	Continuing ('000)
6.8 M				
5 Y	610	350	270	190
10 Y	450	250	220	150
15 Y	400	230	190	100
5.4 M				
5 Y	*		480	90
10 Y	670	100	320	40
15 Y	540	40	260	20

*Reduction scenario not possible

Table 2. Annual removals needed to reduce the population from current levels to 6.8 or 5.4 million within a period of 5, 10 or 15 years, assuming future reproductive rates and Greenland harvest follow a density-dependent manner (Model B). Annual catches were assumed to comprise 90%, or 50% young of the year (YOY). Continuing removals represent the total annual removals allowed that would maintain a 95% likelihood that the population would remain above the limit reference level (N_{30}) for 15 years.

Fixed	90%YOY		50%YOY	
	Reduction ('000)	Continuing ('000)	Reduction ('000)	Continuing ('000)
6.8 M				
5 Y	560	560	250	280
10 Y	420	500	200	260
15 Y	370	500	180	270
5.4 M				
5 Y	*		560	250
10 Y	860	400	400	200
15 Y	770	300	350	170

*Reduction scenario not possible

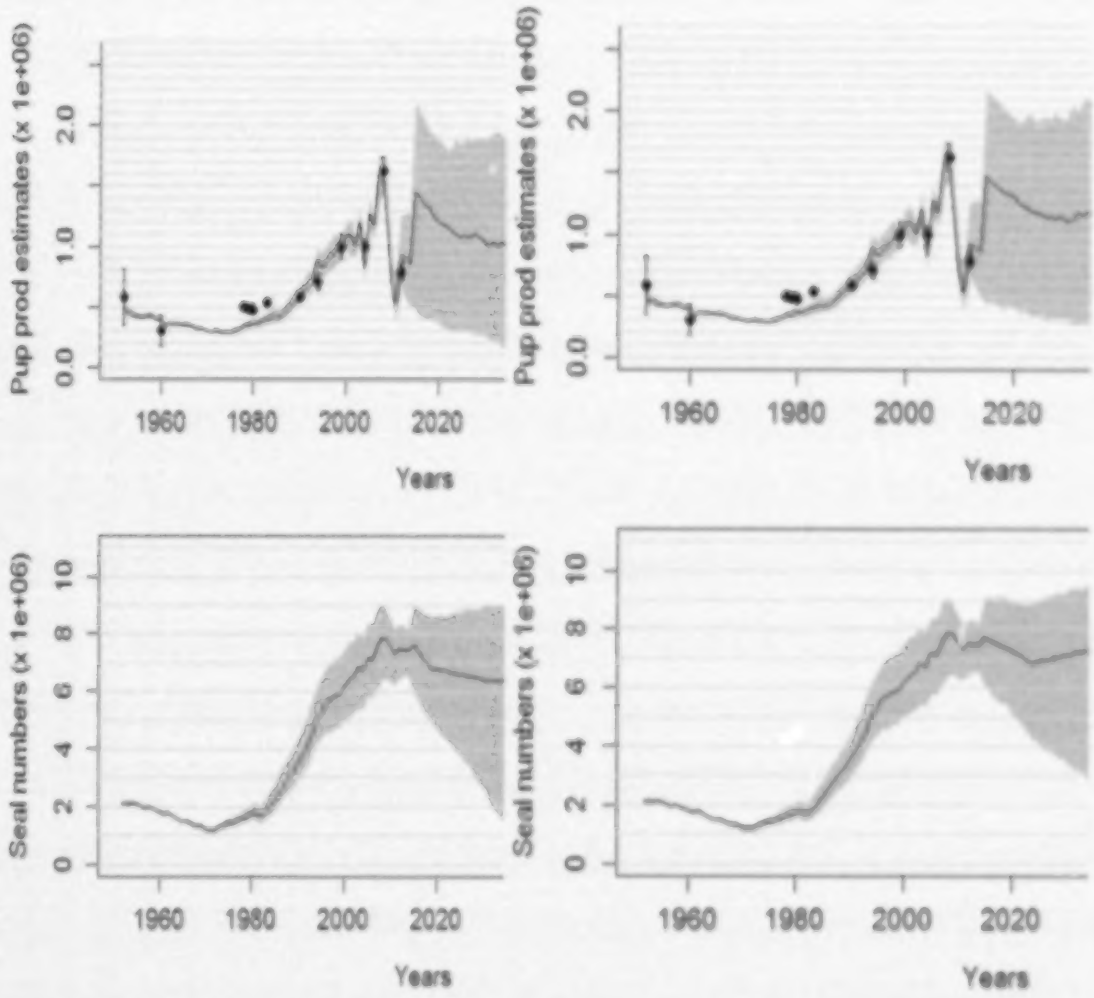


Figure 1a. Trajectory of pup production and total population when reduced to 6.8 million animals over 5 years (left panel) or 10 years (right paned) with a harvest composition of 90% Young of the Year (YOY) (see Table 1). Future reproductive rates and Greenland harvests are assumed to be similar to that seen over the past decade (Model A). Once the population was reduced to the target levels, harvests were reduced to meet the management objective (i.e. ensuring a 95% probability of remaining above the Limit Reference Level of 2.4 million animals). The black line shows changes in mean abundance, the grey shaded areas identify the 95% confidence intervals.

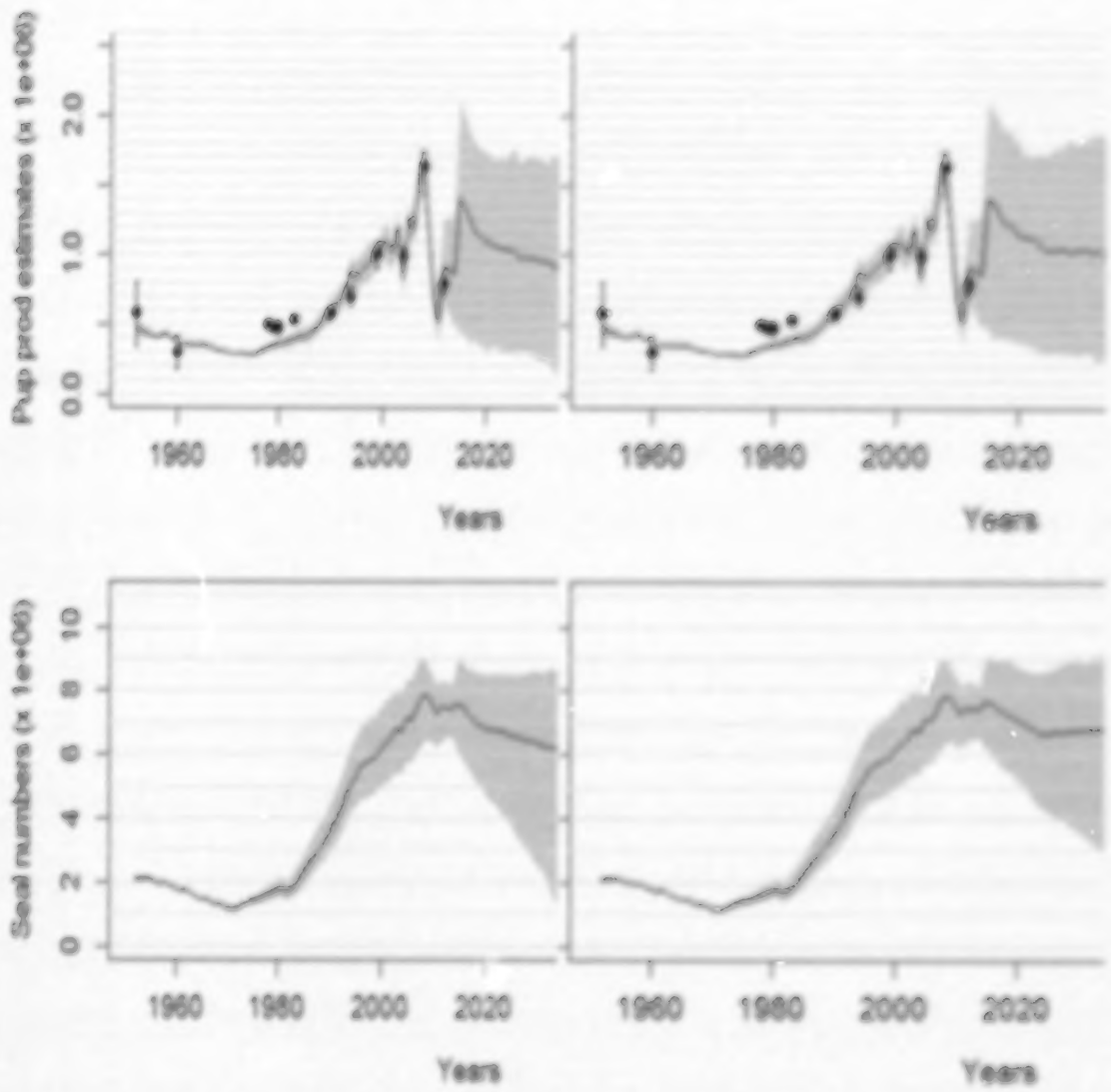


Figure 10. Trajectory of pup production and total population when reduced to 6.8 million animals over 5 years (left panel) or 10 years (right panel) with a harvest composition of 50% Young of the Year (YOY) (see Table 1). Future reproductive rates and Greenland harvests are assumed to be similar to that seen over the past decade (Model A). Once the population was reduced to the target levels, harvests were reduced to meet the management objective (i.e. ensuring a 95% probability of remaining above the Limit Reference Level of 2.4 million animals). The black line shows changes in mean abundance, the grey shaded areas identify the 95% confidence intervals.

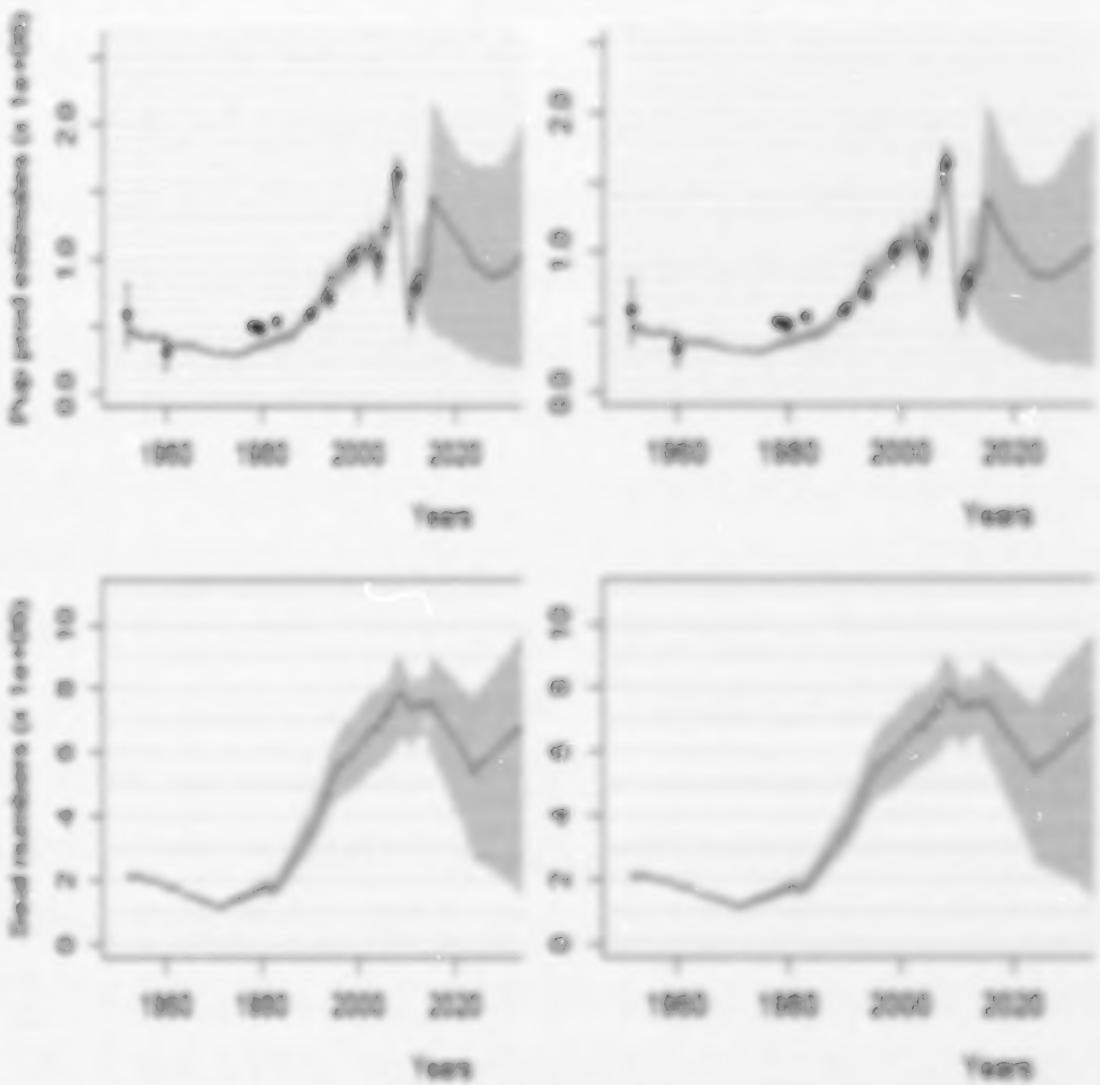


Figure 1c. Trajectory of pup production and total population when reduced to 5.4 million animals over 10 years with a harvest composition of 80% Young of the Year (left panel) (YOY)or 50% YOY (right panel) (see Table 1). Future reproductive rates and Greenland harvests are assumed to be similar to that seen over the past decade (Model A). Once the population was reduced to the target levels, harvests were reduced to meet the management objective (i.e. ensuring a 95% probability of remaining above the Limit Reference Level of 2.4 million animals). The black line shows changes in mean abundance, the grey shaded areas identify the 95% confidence intervals.

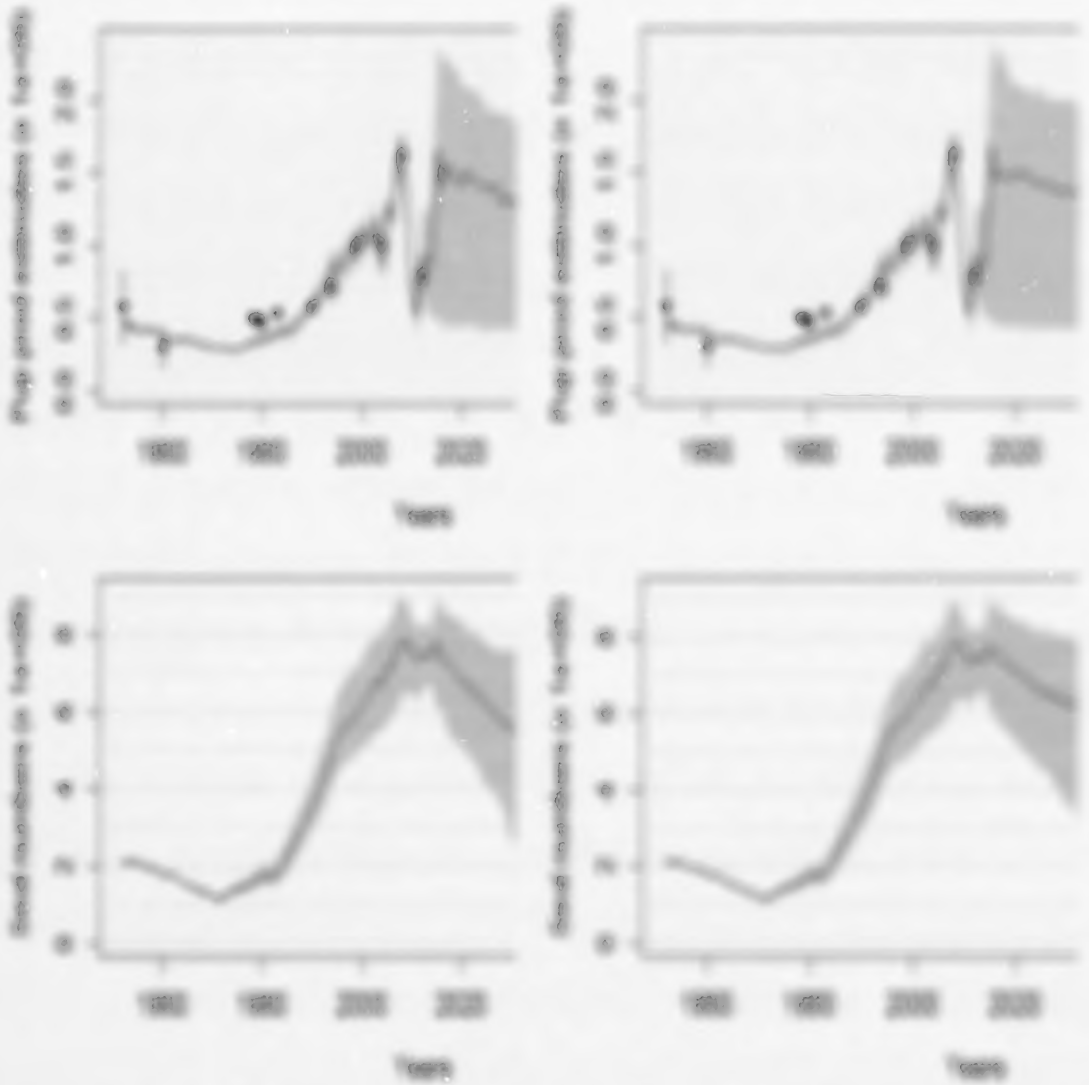


Figure 3a. Trajectory of pup production and total population when reduced to 5.6 million animals over 5 years (left panel) or 10 years (right panel) with a harvest composition of 80% Young-of-the-Year (YOY) (see table 2). Future reproductive rates and Greenland harvests are assumed to a density dependent relationship (Model B). Once the population was reduced to the target levels, harvests were reduced to meet the management objective (i.e. ensuring a 95% probability of remaining above the Limit Reference Level of 2.4 million animals). The black line shows changes in mean abundance, the grey shaded areas identify the 95% confidence intervals.

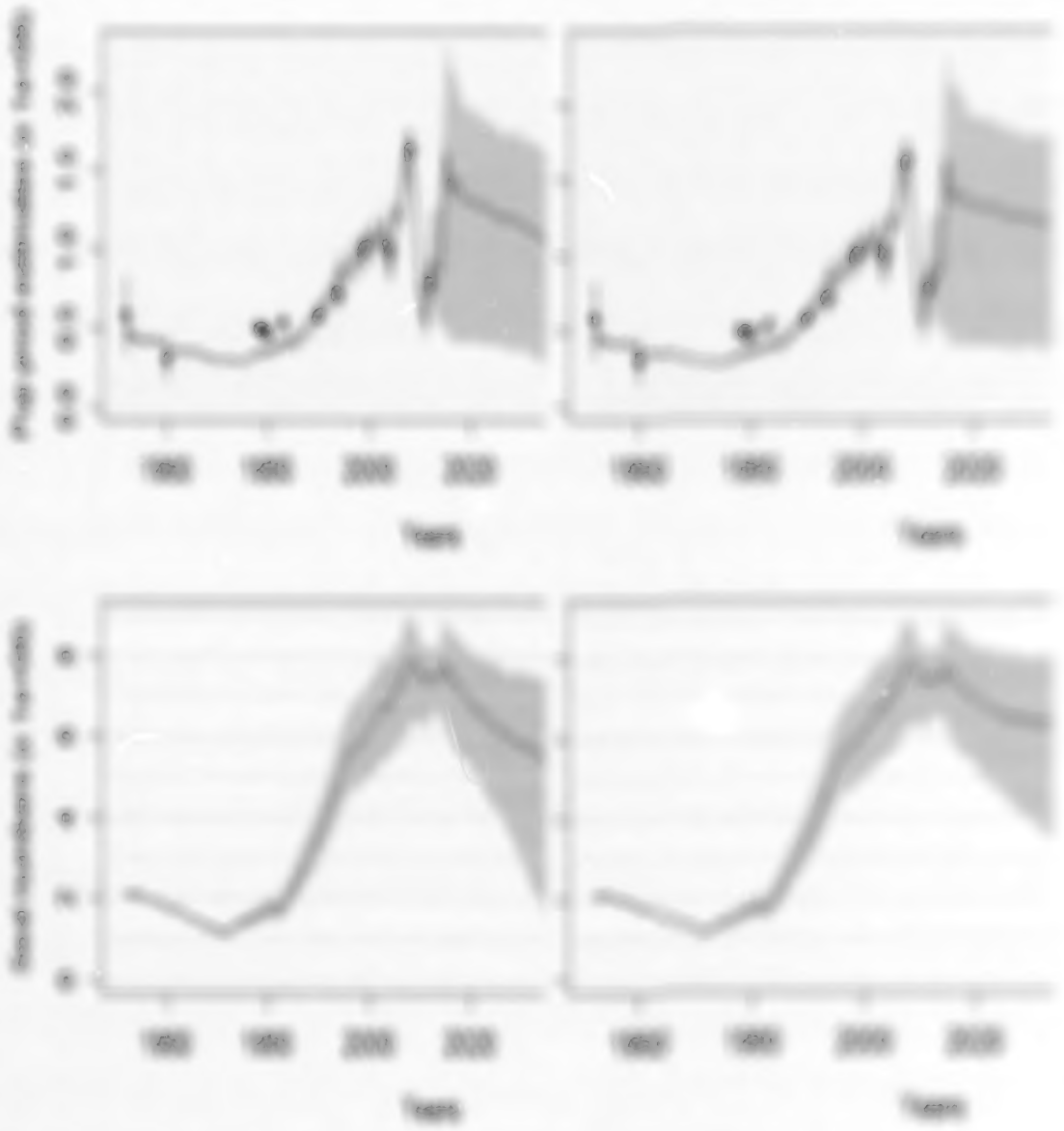


Figure 3b. Trajectory of carp production and total population when [illegible] 6.5 million animals over 3 years (left panel) or 10 years (right panel) with a fish-level composition of 90% [illegible] (top row) and 70% (see table 3). Future reproductive rates and [illegible] are assumed to be density-dependent (Model B). Once the population was restored to the target levels, optimized rates ensured it met the management objective (i.e. ensuring a 90% probability of remaining above the cost fisheries cost of 2.4 million animals). The black line shows changes in mean abundance; the grey shaded area denotes the 90% confidence intervals.

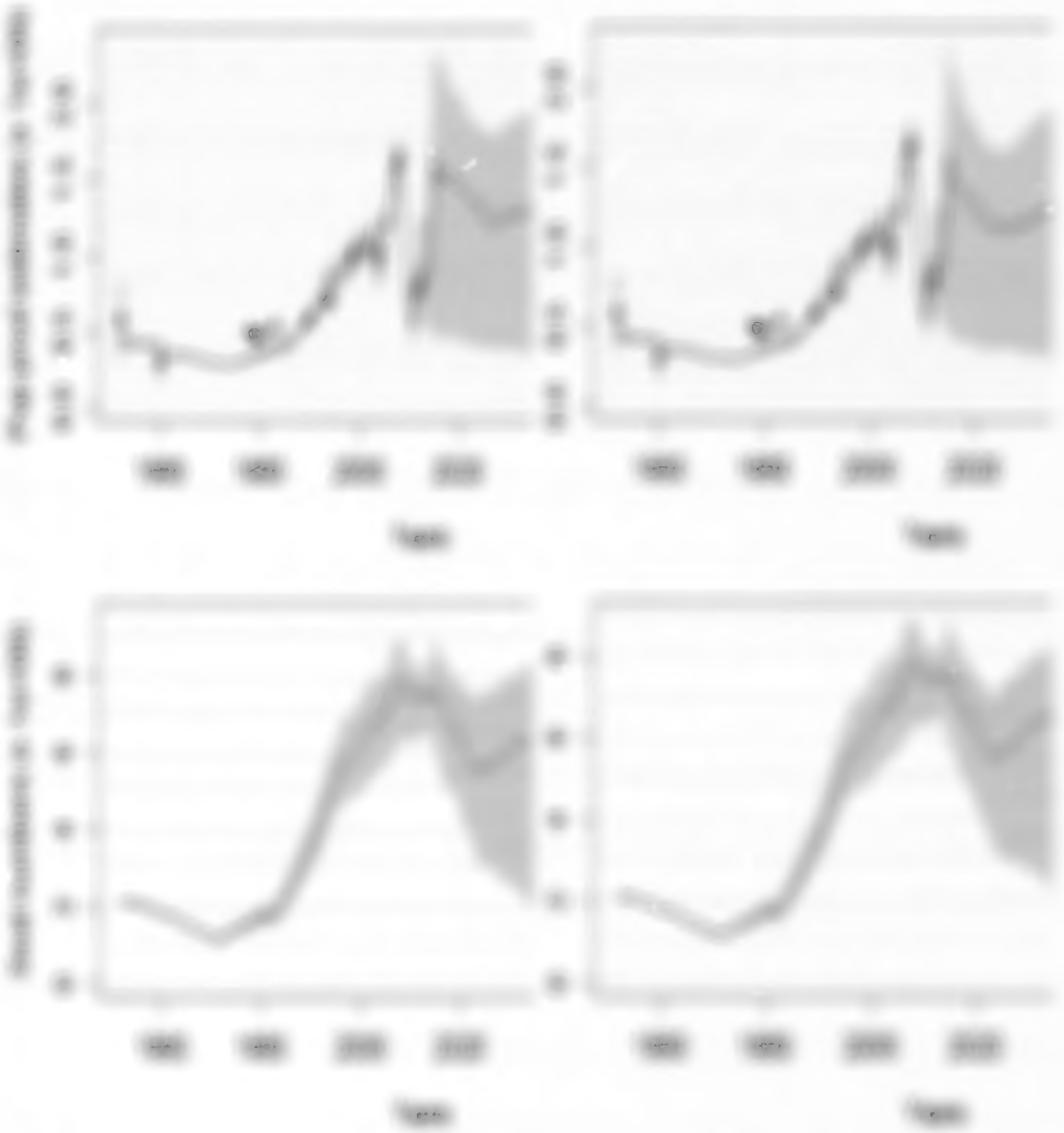


Figure 4A. Trajectories of [illegible] and total population status measured in [illegible] under [illegible] over 10 years. [illegible] Trajectories of [illegible] Total [illegible] [illegible] [illegible]

[illegible]

[illegible] [illegible] [illegible] [

Year	Population, Mean (SD), age	Measurements, data	Population, Cohen's d	Significant findings
[illegible]	[illegible]	[illegible]	[illegible]	
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Appendix 2. Pup production estimates used as input into the population model.

Year	Estimate	Standard Error	Reference
1951†	6e5,000	322,000[‡]	Sergeant and Fisher 1960
1960	235,000	117,000[‡]	Sergeant and Fisher 1960
1978	457,000	34,000	Roff and Bowen 1986
1979	478,000	35,000	Roff and Bowen 1986
1980	475,000	47,000	Roff and Bowen 1986
1983	524,000	33,000	Bowen and Sergeant 1988
1988	577,000	36,000	Stenson et al. 1993
1994	702,000	63,000	Stenson et al. 2002
1999	997,000	132,100	Stenson et al. 2003
2004	991,400	98,200	Stenson et al. 2005
2008	1,600,000	110,400	Stenson et al. 2010
2012	791,040	63,000	Stenson et al. 2016a

[‡] Assumed a coefficient of variation of 40%.

Appendix 3. Year, sample size (n), number pregnant (#preg) and late term age-specific reproductive rates of Northwest Atlantic harp seals.

Age	4		5		6		7		8+	
Year	*n*	#Preg	*n*	#Preg	*n*	#Preg	*n*	#Preg	*n*	#Preg
1954	4	0	3	1	3	2	16	12	33	29
1964	11	0	9	1	2	1	4	3	25	22
1965	30	1	44	5	37	20	38	27	109	96
1966	7	0	9	1	17	6	11	8	49	43
1967	10	0	19	4	33	20	29	28	123	109
1968	27	0	19	6	20	14	12	11	55	48
1969	25	1	25	4	16	7	28	23	165	146
1970	13	0	13	3	12	6	10	9	107	92
1978	40	1	38	23	20	18	9	6		
1979	21	5	15	8	5	5	9	8	21	20
1980	2	0	2	1	1	1	0		12	9
1981	5	1	4	3	2	1	7	6	17	14
1982	4	0	5	2	1	1	4	3	3	1
1985	4	0	3	1	5	2	3	3	1	1
1986	1	1	0		2	1	1	0	7	7
1987	12	2	8	3	9	7	4	4	24	15
1988	17	2	6	1	3	3	0		19	14
1989	8	0	9	0	6	2	3	2	22	22
1990	8	0	7	1	3	1	1	0	10	6
1991	10	0	11	2	7	4	3	1	29	18
1992	10	2	11	3	9	4	8	6	32	21
1993	11	1	17	2	7	0	5	4	35	17
1994	23	1	16	2	14	6	7	3	41	34
1995	10	0	13	6	4	2	5	2	24	14
1996	8	0	6	0	4	1	1	1	35	24
1997	6	0	4	0	10	3	2	2	36	27
1998	6	0	10	3	9	2	4	2	36	22
1999	6	0	7	0	18	4	15	6	59	37
2000	1	0	9	3	6	4	5	2	43	29
2001	2	0	0		2	2	3	0	39	26
2002	2	0	4	1	5	3	17	10	72	40
2003	1	0	3	2	2	1	3	2	91	59
2004	2	0	5	0	5	1	1	0	76	31
2005	9	1	9	0	13	2	7	0	86	55
2006	2	0	0		0		0		119	67
2007	1	0	5	0	3	1	2	2	84	64

Age	4		5		6		7		8+	
Year	*n*	#Preg	*n*	#Preg	*n*	#Preg	*n*	#Preg	*n*	#Preg
2008	6	0	3	0	2	0	0		61	45
2009	1	0	1	0	1	0	1	1	103	57
2010	3	0	0		0		1	0	116	34
2011	3	0	2	1	0		0		147	30
2012	0		1	0	0		0		20	15
2013									6	5

Appendix 4. Removals of Northwest Atlantic harp seals from different sources taken from Stenson 2014.

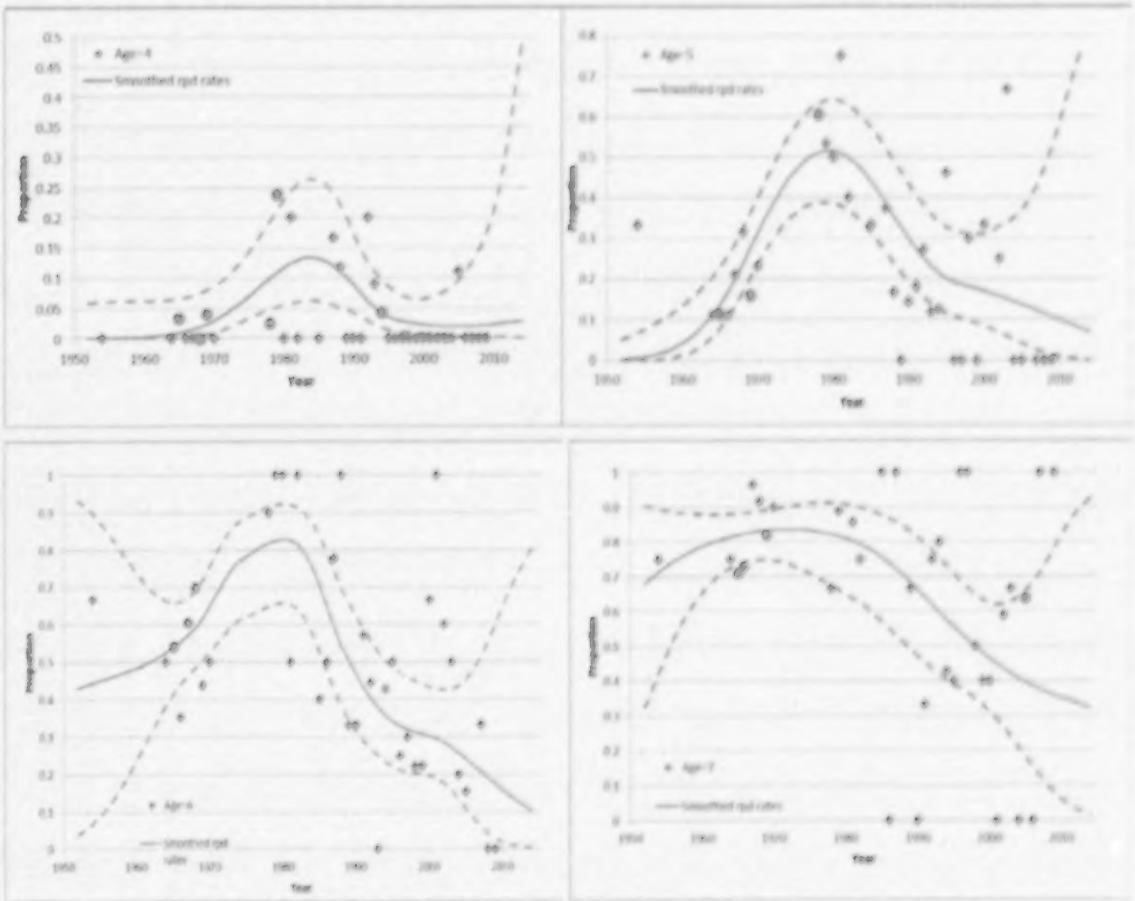
Year	Arctic	Greenland	Commercial (Age =0)	Commercial (Age=1+)	Bycatch (Age=1+)	Bycatch (Age=0)
1952	1,784	16,400	198,063	109,045	0	0
1953	1,784	16,400	197,975	74,911	0	0
1954	1,784	19,150	175,034	89,382	0	0
1955	1,784	15,534	252,297	81,072	0	0
1956	1,784	10,973	341,397	48,013	0	0
1957	1,784	12,884	165,438	80,042	0	0
1958	1,784	16,885	140,996	156,790	0	0
1959	1,784	8,928	238,832	81,302	0	0
1960	1,784	16,154	156,168	121,182	0	0
1961	1,784	11,996	168,819	19,047	0	0
1962	1,784	8,500	207,088	112,901	0	0
1963	1,784	10,111	270,419	71,623	0	0
1964	1,784	9,203	266,382	75,281	0	0
1965	1,784	9,289	182,758	51,495	0	0
1966	1,784	7,057	251,135	72,004	0	0
1967	1,784	4,242	277,750	56,606	0	0
1968	1,784	7,116	156,458	36,238	0	0
1969	1,784	6,438	233,340	55,472	0	0
1970	1,784	6,269	217,431	40,064	15	53
1971	1,784	5,572	210,579	20,387	99	391
1972	1,784	5,994	116,810	13,073	141	480
1973	1,784	9,212	98,335	25,497	107	358
1974	1,784	7,145	114,825	32,810	41	141
1975	1,784	6,752	140,638	33,725	66	219
1976	1,784	1,1956	132,085	32,917	169	923
1977	1,784	1,2866	126,982	28,161	296	1,281
1978	2,129	1,6638	116,190	45,533	538	2,381
1979	3,620	17,544	132,458	28,083	511	2,799
1980	6,350	15,255	132,421	37,105	263	2,454
1981	4,672	22,974	178,394	23,775	382	3,539
1982	4,881	26,926	145,274	21,465	343	3,442
1983	4,881	24,784	50,058	7,831	458	4,504
1984	4,881	25,828	23,922	7,622	425	3,683
1985	4,881	20,785	13,334	5,701	632	4,225
1986	4,881	26,098	21,888	4,046	1,042	7,136
1987	4,881	37,859	36,350	10,446	1,978	11,118
1988	4,881	40,415	66,972	27,074	1,391	7,154
1989	4,881	42,970	56,346	8,958	799	9,457
1990	4,881	45,526	34,402	25,760	921	2,700
1991	4,881	48,082	42,382	10,206	615	9,074
1992	4,881	50,638	43,866	24,802	6,507	18,969
1993	4,881	56,319	16,401	10,602	7,596	18,876
1994	4,881	57,373	25,223	36,156	10,513	35,881
1995	4,881	62,749	34,106	31,661	6,060	13,641
1996	4,881	73,947	184,856	58,050	18,347	10,765
1997	2,500	68,815	220,476	43,734	5,059	13,541

Year	Arctic	Greenland	Commercial (Age =0)	Commercial (Age=1+)	Bycatch (Age=1+)	Bycatch (Age=0)
1998	1,000	81,272	251,403	31,221	975	3,571
1999	500	93,117	237,644	6,908	6,312	9,799
2000	400	98,458.5	85,035	7,020	1,611	9,736
2001	600	85,427.5	214,754	11,739	4,847	14,628
2002	1,000	66,734.5	297,764	14,603	3,837	5,492
2003	1,000	66,149	280,174	9,338	1,881	3,486
2004	1,000	70,585.5	353,553	12,418	3,890	8,703
2005	1,000	91,695.5	323,800	6,029	3,807	8,518
2006	1,000	92,210	346,426	8,441	3,816	8,539
2007	1,000	82,836	221,488	3,257	3,845	8,602
2008	1,000	80,556	217,565	285	3,924	8,780
2009	1,000	72,142	76,688	0	3,946	8,829
2010	1,000	90,014	68,654	447	3,884	8,691
2011	1,000	74,013	40,371	18	3,883	8,688
2012	1,000	79,912[1]	71,319	141	3,883	8,688
2013	1,000	79,912[1]	90,703	0	3,883	8,688

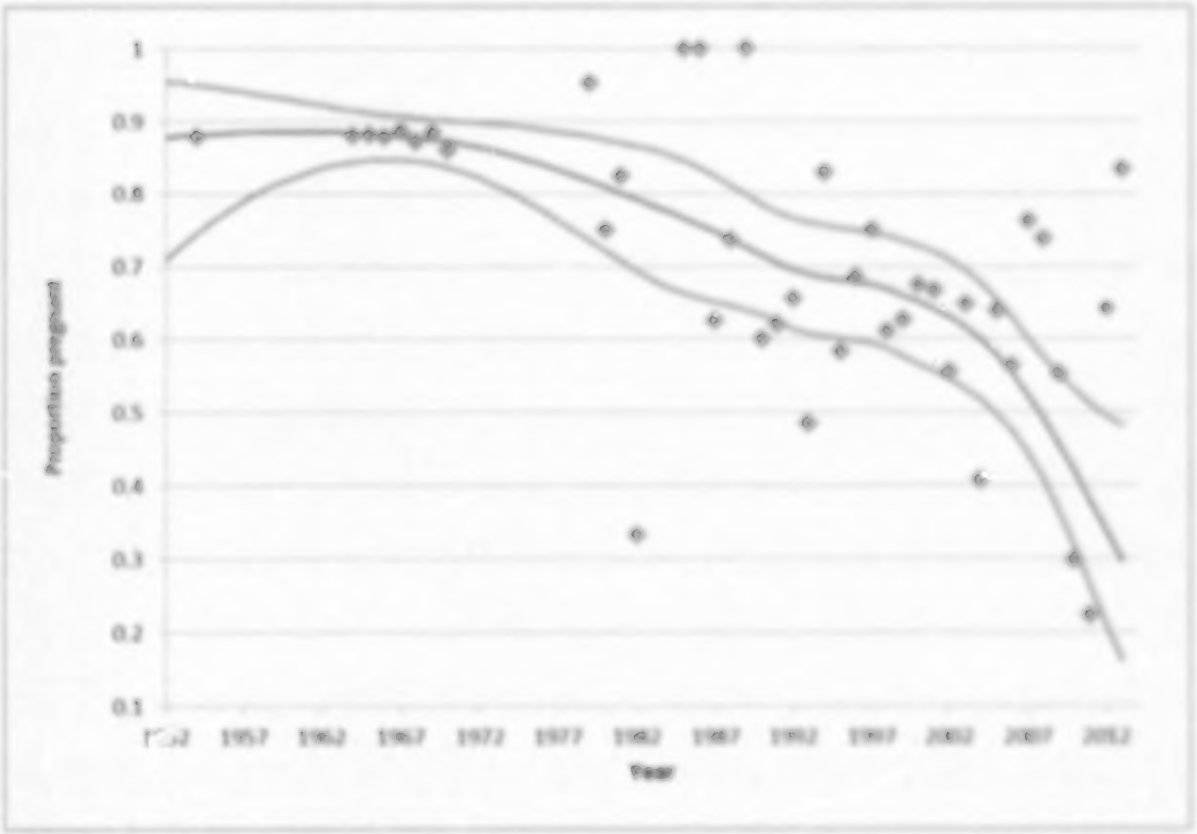
[1] *average of last 5 years.*

Appendix 5. Years when unusual ice mortality is assumed to have occurred, and values input to the model to account for this mortality. Survival was assumed to be normal (i.e. 1.0) in all other years. 2013 estimates were taken from Hammill and Stenson (2014). Data are missing from the ice charts for 1970. This value was set to 1.

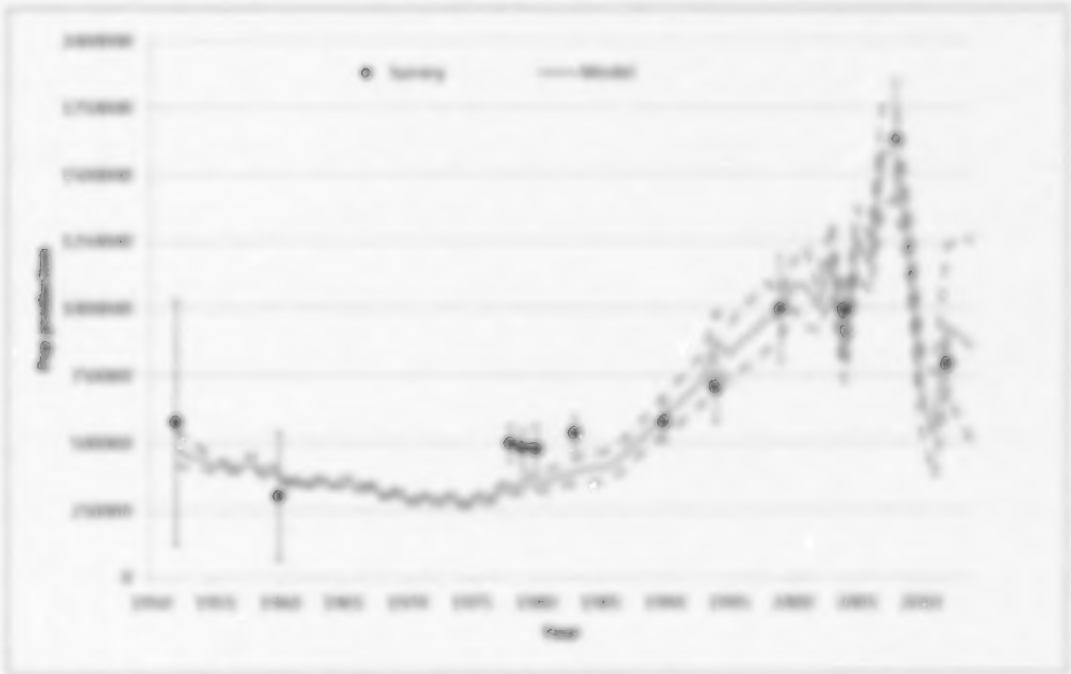
Year	Survival (prior to 2012)	2012 survival estimates (updated)	2013 survival estimates
1969	0.75	0.43	0.35
1970			1
1978			0.92
1981	0.75	0.19	0.32
1996			0.93
1998	0.94	0.91	0.83
1999			0.94
2000	0.88	0.87	0.8
2002	0.75	0.83	0.88
2005	0.75	0.76	1.0
2006	0.90	0.99	0.86
2007	0.78	0.91	0.85
2010	0.55	0.41	0.71
2011		0.3	0.35
2012		0.83	0.77
2013		0.90	0.77



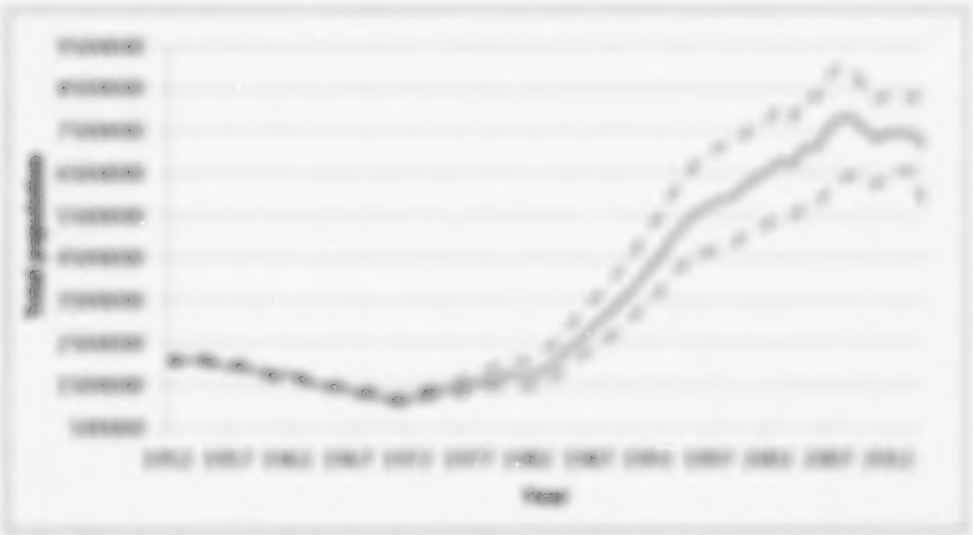
Appendix 6. Age specific reproductive rates and non-parametric smoothed rates for ages 4 to 7 years. Diamond (blue) symbols represent data points based on less than 20 samples, round (red) symbols represent samples where there were 20 or more samples.



Appendix 6 (continued). Age specific reproductive rates, non-parametric smoothed rates and predicted reproductive rates if determined by density-dependent factors only for animals aged 8+ years.



Appendix 7a. Estimated annual pup production for model fitted to pup survey estimates (mean ± 95% CI) and reproductive data up to and including 2013 (left Y-axis). Also presented are reported catches (right Y-axis).



Appendix 7b. Estimated population trajectory for model fitted to pup survey estimates (mean ± 95% CI) including the 2012 estimates and reproductive data up to and including 2012 (last 7 years). Annual reported catches (purple) are also included (right Y-axis).